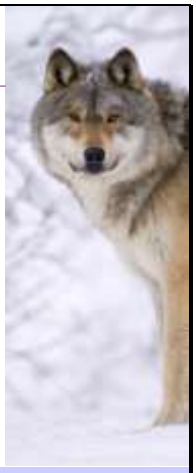
Behavioral Ecology of Vertebrates



Unit 6. Groups

Module 3. Social

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Learning, Discovering and Sharing Knowledge

In the previous module, we looked at several aspects of how the habitat influences individual decisions about obtaining resources. Now we will look more at how the social environment influences these decisions. By focusing in on those few species who live in social groups, we will be discussing how access to resources and risks may be modified by the social context.

Learning Objectives (Davies et al. 2012:177)

Costs and benefits of living in groups:

1. **Anti-predator adaptations**: dilute risk of attack, predator confusion, communal defense, group vigilance
2. **Foraging adaptations**: searching, prey capture, sharing food, individual variation (skew), delayed breeding
3. **Complex group movements**: shoaling, traffic lanes, individual local rules, leadership, voting

As we established in Module 1 of this course, cost/benefit analysis is the primary way that researchers examine behavioral adaptations associated with group living. In the past two decades, most of this research has been in the categories of anti-predator behavior and foraging. The most exciting new research is emerging in the category of complex group movements emerge from the local decisions of many individuals.

Davies et al. 2012, Fig 6.4

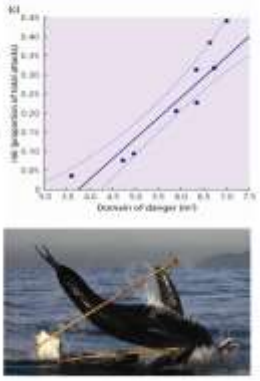
Individual benefits of hiding in a group

1. ANTI-PREDATOR ADAPTATIONS

Geometry of the "selfish herd" is one of the classic models that attracted a lot of attention, maybe because of its catchy name. It addresses the benefits of "hiding in a group", suggesting that individuals make decisions based on reducing the "domain of danger". In this diagram the darkest frog has the largest domain of danger (blue line). If the frog jumps to the position of the ghost frog (white), the domain of danger will be reduced. The frog on the far left would have been edited out of the population. However, there are other models addressing anti-predator adaptations of animals living in groups.

1.1 Dilute risk (Davies et al. 2012:152)

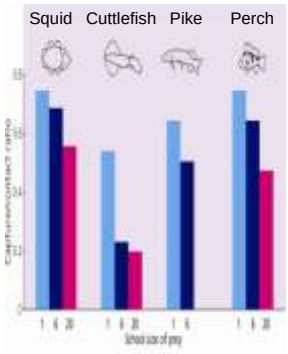
- **H1**. Risk of attack reduced when individuals are grouped close together
- Set out seal decoys, towed as a raft = trigger shark attack
- Treatment:
  - Short domain of danger (decoys close)
  - Long domain of danger
- Risk correlated with DOD



Lets look closer at the idea that grouping behavior is an anti-predator adaptation because the risk of attack is diluted . This ingenious experiment used models of seals as decoys for sharks. The distance between the decoys was the "domain of danger" (DOD).

1.2 Predator confusion (Davies et al. 2012, Fig 6.5)

- **H1**: prey in larger groups confuse predator
- Ambush predators: 3
- Chase predator: *perch*
- Treatment:
  - Prey group: 1, 6, 20
- Predators more successful targeting smaller groups
- Perch "switched targets"



The "predator confusion" effect may be hard to separate from the "dilution effect". This is a study that helped to clarify the distinction.

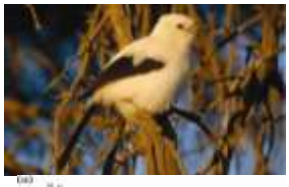
1.3 Communal defense (Davies et al. 2012:154)

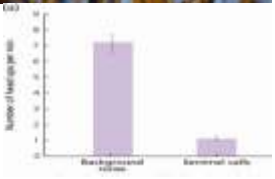
- Guillemots nest in colonies
  - Attack predators
  - Nest success better in dense colonies
- Field-fare thrushes
  - Artificial nests survived better near colony
- **Chat Q: What other species would illustrate this concept?**

Living in groups may also be adaptive for prey who "fight back". These are two classic examples of colony nesting birds. However, there are also many examples of large ungulates who fight back. I am thinking of cape buffalo in Africa and musk oxen in North America.

1.4 Improved vigilance (Davies et al. 2012:158)

- "Watchman's song"
- Pied babblers switch to sentinel tactic when satiated
- **H1:** reduced individual vigilance with sentinel calls *(foraged more)*
- Treatment: playback experiment
- **Chat Q: other species?**





"Vigilance" is another hypothesis . This is a study of the use of playbacks to test the positive effects of a sentinel . | Other species? Meerkats Vigilance has also been examined in winter flocks of passerines and elk in Yellowstone.

1.4 Poll- lets see if you understand

Exploitation competition: which of these topics would you like to chat more about?

a) Dilution reduces risk- "domain of danger"
b) Predator confusion- "switch targets"
c) Communal defense- fight back
d) Improved vigilance with many eyes
e) I'm good, lets move on

Davies et al. 2012, Fig 6.13

Costs & benefits of foraging in groups

2. FORAGING ADAPTATIONS

Now lets switch from the perspective of the prey to the predators who hunt in groups. There are costs as well as benefits. CHAT Q: notice anything strange about the sex of the lions attacking this cape water buffalo? (Usually it is the females that kill the prey and the males come in for the meal)

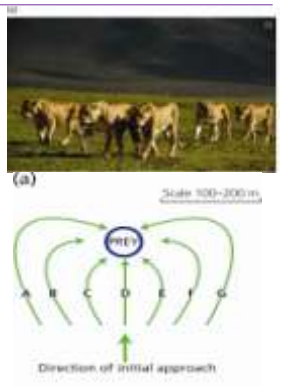
2.1 Search- info transfer (Davies et al. 2012:160)

- H1: Recruitment Center – ravens
  - Search independently, return to roost
  - Recruit others- protection from predators and competitors
  - Don't recruit if food is not sharable
- H2: Eavesdropping Center- egrets
  - Benefits scrounger more than producer
  - Anonymous assemblage- unrelated

One of the earliest ideas about the benefits of living in a group was the "Information Center" hypothesis. | This was critiqued and resulted in two better hypotheses that are now being tested.

2.2 Capture "teams" (Davies et al. 2012: 162)

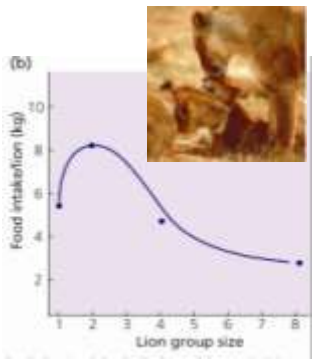
- **H1**: individuals learn tactics for group hunting large prey *(wildebeest)*
- "wings" circled the prey, stalked, initiated attack, run prey toward centers
- "centers" waited in ambush, larger lionesses better at killing prey
- Not all groups are teams



Another hypothesis is that in stable groups individuals learn what to expect from each other. Benefits are in taking down prey much larger or faster than an individual could capture.

2.3 Food sharing (Davies et al. 2012:164, Fig. 6.18)

- H1: capture success increases with group size *(benefit)*
- H2: food intake per lion decreases *(cost)*
- Switcher strategy
  - Bider tactic- stay home
  - Disperser tactic- leave
  - Joiner tactic- conditional on improving access to resources (food, mates)



A cost of foraging in a group is that you have to share with others at the "dinner table".

2.4 Individual variation (Davies et al. 2012, Fig 6.20)

- H1: Skew in benefits
  - Some individuals have more access to resources
  - Affects size-based "eviction"
- Switcher tactics
  - Don't eat, stay small & wait
  - Eat, grow & face conflict
  - Escalate to same-size fish
  - Leave breeding group
- Also: clownfish, wolves, banded & dwarf mongoose

Coral-dwelling goby

More recently, researchers are looking at how not all individuals "at the table" receive the same amount of food. | This has implications for delayed reproductive maturity and how long a competitor may "hide in plain sight" before eviction by a dominant breeder.

2.5 Poll- lets see if you understand

About which of the previous topics would you like to chat more?

a) Large groups search better – more eyes
b) Large groups capture larger prey
c) Sharing large food items
d) Individual variation- "excluded from the table"
e) I'm good, lets move on

Lets dialogue more about this using the elearning discussion tool

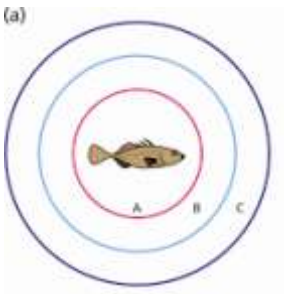
Davies et al. 2012 Fig. 6.1

Individual decision rules influence group

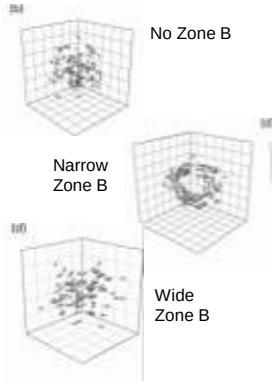
3. COMPLEX GROUP MOVEMENTS

Some of the most exciting studies of group living are focusing on how the behavior of the group is an emergent property resulting from many local decisions made by individuals.

3.1 Local decisions (Davies et al. 2012, Fig. 6.22)



RULES:
Zone A: move away
Zone B: orient
Zone C: move toward

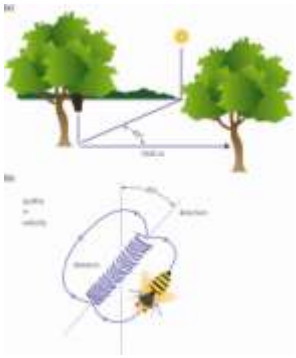


This is most clearly illustrated by models of the shoaling behavior of fish.

3.2 Group voting (Davies et al. 2012, Fig. 6.25)

- A few individuals within a group can lead the entire group to a new resource *(food or nest cavity site)*
  - It does not involve complex communication- dance language
  - Group makes final decision by opinion polling (voting process)
- Honeybees use opinion polling to find a new nest site
  - Scouts search for and inspect new nest sites
  - Return to the nest to perform waggle dance to provide information about the new site
  - The dance indicates the location and the quality of the new site

(Franks et al. 2002)



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Hypotheses about how individual decisions influence groups have been test elegantly in honeybee colonies. This applies to recruiting foragers to a rich nectar source as well as choice of a new cavity for a swarm to start a new colony.

3.2 Group voting (con't) (Davies et al. 2012: 175)

- Many scouts perform the dance for different sites
- Dances showing high quality sites may have other scouts inspect those sites
  - They will then perform a new dance indicating the quality of the site
  - Therefore, the scouts may switch sites based on dances performed by others
- Generally, when a dance for one particular high quality site is performed by the majority of the scouts, then the opinion polling ends- "consensus"
  - The swarm follows the scouts to the new location
  - The "winning" site excites the most scouts
- Additional reading: (Franks et al. 2002)
- **CHAT Q: Is this a group or individual decision?**

Credits: J. Carbaugh (edited by J. Packard)

3.3 Opinion polling (Davies et al. 2012:174)

Species	Decision	Behavior
Ant *Temnothorax*	Choice of new nest site	Workers recruited by tandem runs and then transport
Whooper swan	When to move after a rest	Head movements
Mountain gorilla	Same as above	"Grunts"
African buffalo	Which direction to move	Stand up and gaze in a particular direction

I like "opinion polling" better than "voting". It is not only in social insects, although they are some of our best examples. The studies on social insects are changing how researchers are framing hypotheses for studies of other vertebrate species.

3.4 Poll- lets see if you understand

About which topic would you like to chat about more?

a) Local decisions- fish shoals
b) Group foraging in honeybees "dance language"
c) Opinion polling in honeybees "group voting"
d) Opinion polling in other species
e) I'm good, lets move on

Lets dialogue more about this using the elearning discussion tool

Summary (Davies et al. 2012:177)

Costs and benefits of living in groups:

1. **Anti-predator adaptations**: dilution, predator swamping, selfish herd, communal defense, vigilance.
2. **Foraging adaptations**: searching, prey capture, sharing food, individual variation (skew), delayed breeding
3. **Complex group movements**: local rules -fish shoaling, foraging recruitment "dance", opinion polls

In this first unit of Module 3, we have looked at the costs and benefits of safety in numbers and access to food, related to living in groups. In the next Unit 7, we will look at competition over mates as resources in social groups. That will set the "stage" for looking at adaptations for parental care in groups in Unit 8.